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SMALLER *OLEA EUROPAEA* FRUITS HAVE MORE POTENTIAL DISPERSERS: IMPLICATIONS FOR OLIVE INVASIVENESS IN CALIFORNIA

CLARE E. ASLAN AND MARCEL REJMÁNEK
Department of Evolution and Ecology, University of California, Davis,
One Shields Avenue, Davis, CA 95616
ceaslan@ucdavis.edu

ABSTRACT

Olea europaea (European olive) is invasive in Australia and widely planted in California. Vertebrates, particularly birds, mediate *Olea* seed dispersal. Fruits are large, but their sizes range widely. We measured fruit widths from 12 study stands in California and constructed esophageal probes in diameters spanning the resulting size range. We then obtained whole-bird frugivorous bird carcasses and used the probes to determine the fruit sizes that each bird species would be anatomically capable of swallowing. This allowed us to develop lists of potential dispersers for each study stand. Even stands with the largest measured fruits had several potential disperser species, but the list of species expanded greatly as fruit sizes decreased. Feral *Olea* stands with remarkably small fruits have been observed in California and Australia. An increase in the incidence of such stands might augment the regional spread rate for the species.

Key Words: Bird-mediated dispersal, European olive, gape width, invasion, museum specimens, *Olea europaea*.

A variety of invasive, or potentially invasive, woody species are dispersed by birds (Richardson et al. 2000; Aslan and Rejmánek 2010). Among these is *Olea europaea* L. (Oleaceae) (European olive, hereafter, *Olea*), an upland species native to the Mediterranean. *Olea* is widely cultivated in California, as well as in other regions similar in climate, as a crop and landscaping species. *Olea* has become invasive in natural areas in Australia, where its fruits are bird-dispersed (Spennemann and Allen 2000b). Field observations have confirmed that birds consume *Olea* fruits in California, as well (Aslan 2010). Since (a) the climate is appropriate for *Olea* establishment, and (b) the species demonstrates dispersal mutualisms with resident birds, a potential incipient invasion by *Olea* in California appears possible.

Effective dispersal of *Olea* (and, by extension, the likelihood of invasion) may be dictated by fruit sizes. *Olea* fruit sizes range enormously (e.g., from a minimum of 5.6 mm to a maximum of 28.2 mm in width for fruits we collected from studied Californian populations). In general, however, the species is large-fruited and seed mass is positively correlated with fruit size (Alcántara 1995), making vertebrate-mediated dispersal necessary for removal of seeds from parental locations. Since the species is cultivated primarily for human food, artificial selection for large fruits has been imposed on *Olea* strains (Rey and Gutiérrez 1996). However, fruit size may constrain seed dispersal. Particularly large fruits of *Olea* and other species are often pecked rather than swallowed whole by birds (Rey and Gutiérrez 1996). This strategy is necessitated by gape width limitations, but appears energetically costly for birds, which prefer to swallow fruits whole when they are able to do so (Rey and Gutiérrez 1996). Fruit pecking transforms a mutualistic relationship into seed predation by rarely promoting effective dispersal beyond the stand canopy (Rey et al. 1997). Among wild olives, therefore, gape width limitations of potential dispersers appear to counteract selective pressures favoring large seeds (e.g., enhanced germination success and greater seedling vigor) and likely dictate seed size maxima (Alcántara and Rey 2003).

Olea was introduced to Australia in 1800 and planted in many locations over the next two centuries, but its profitability as a crop species was generally low, and most olive stands were abandoned (Hartmann 1962; Spennemann and Allen 2000b). Fruit and seed sizes in feral *Olea* populations in Australia are reportedly smaller than those of cultivated orchards (Spennemann and Allen 2000a). Size reduction in self-seeded populations that are geographically separated from any parent stand may result from one of two mechanisms: lack of anthropogenic cultivation and care in the early stages of stand establishment, or selection of smaller fruits by birds. Care (in the form of irrigation, pruning, fruit harvesting, or fertilization) is no longer provided in abandoned olive stands in Australia nor in our study stands in California, all of which are old and established as hedgerows rather than orchards; however, at least some irrigation was likely performed at initial planting in both countries. The phenomenon of fruit size reduction following disperser-mediated selection has been observed for palm seeds following toucan

TABLE 1. *OLEA EUROPAEA* STUDY STANDS AND RELEVANT CHARACTERISTICS.

Study stand (ranked by minimum fruit size)	Location	Land-use type	Varietal	Feral
1	Chico	Semi-natural	Mission	Yes
2	Chico	Semi-natural	Mission	No
3	Chico	Urban	Mission	No
4	BCCER	Semi-natural	Mission	No
5	PC	Agricultural	Manzanillo	No
6	Davis	Agricultural	Manzanillo	No
7	PC	Agricultural	Manzanillo	No
8	Davis	Agricultural	Manzanillo	No
9	BCCER	Semi-natural	Mission	No
10	Davis	Urban	Manzanillo	No
11	PC	Agricultural	Manzanillo	No
12	Davis	Urban	Manzanillo	No

exclusion (Galetti et al. 2010), while birds in a Spanish woodland selected *Prunus mahaleb* L. fruits that were significantly smaller on average than the mean size of available fruits (Jordano 1995). Furthermore, minimum fruit size was found to be more predictive of dispersal interactions than was average fruit size in a network of frugivores and large-seeded fruit in New Zealand (Kelly et al. 2010), implying that fruits small enough for ingestion were attractive even when they were surrounded by larger seeds. Logically, fruit size is likely to decrease following these selective pressures, and the suites of vertebrate species able to potentially disperse olive seeds may grow as a result (Spennemann and Allen 2000a). Theoretically, then, rates of dispersal and invasion may escalate as feralization continues.

In California, spontaneous spread of *Olea* is presently rare; we know of only two completely feral and reproductive populations of *Olea* at this time. Since *Olea* stands in California exhibit a range of fruit and seed sizes, we expect that the bird-mediated dispersal potential of different stands varies according to those sizes. Most *Olea* individuals, cultivated in orchards, have large fruits and receive irrigation, fertilizer, and pruning. Outside of orchards, many trees in old hedgerows that receive little care today but were likely irrigated at planting also exhibit large fruits. We hypothesize that dispersal of seeds from such trees is possible for only a limited number of bird species and is therefore relatively rare. We have, however, identified several *Olea* stands (generally planted for landscaping rather than crop purposes) with fruits that are quite small. We hypothesize that a wider diversity of bird species are capable of dispersing these fruits.

As a general rule, decreasing bird body size shows a slight but significant correlation with increasing population density across species (Juanes 1986). As olive fruits shrink and birds of smaller body size are capable of consuming them, the number of individual birds capable of dispersing fruits should increase at a greater rate than the number of disperser species. Correspondingly, dispersal potential itself will grow at an accelerating rate.

Due to both of these increases (increased diversity and increased population sizes) among disperser birds, we consider it likely that expanded suites of potential dispersers will result in greater dispersal, possibly creating small-seeded and small-fruited feral populations as has likely occurred in Australia (Spennemann and Allen 2000b). The appearance and multiplication of such feral populations in California might signify the beginning of a large-scale invasion by this species.

Here, we used esophageal probes and Californian bird carcasses to identify the suites of bird species that are likely capable of swallowing *Olea* fruits of varying sizes. We compare the diversity of birds comprising each suite and discuss the probable implications of fruit size reduction for *Olea* invasiveness.

METHODS

Study Species: *Olea europaea*

In California, *Olea* occurs in at least 27 counties (Calflora 2010) and is valued at more than $86 million as an agricultural commodity (CDFA 2008). For this study, we examined fruits from *Olea* stands in Yolo and Butte Counties in north-central California. Among the 12 focal stands, three were located in urban areas (Chico 3, Davis 3, and Davis 4), five in agricultural areas (Davis 1, Davis 2, PC 1, PC 2, and PC 3), and four in semi-natural areas (an abandoned homestead (BCCER 1 and 2), a municipal protected area (Chico 2) and one completely feral population in a previously-grazed, protected canyon (Chico 1) (Table 1). None of the study stands currently receive irrigation or fertilization.

Esophageal Fruit Passage Assessment

In January, 2009, we collected 10 ripe olives from each of up to 12 trees per study stand, for a total of 60–120 olives from each of the 12 study stands. We used digimatic (Mitutoyo America Corporation, Aurora, IL) calipers to measure the width of each olive to the tenth of a millimeter. We calculated the mean, minimum, and maximum fruit widths for each population. Transverse diameter (width) was utilized because it is likely to be the limiting dimension determining the maximum size of fruits that can be swallowed whole (Wheelwright 1985). We examined the relationship between fruit sizes and land use type using ANOVA.

We then constructed gape width probes to determine which bird species are likely physically capable of swallowing average- and minimum-sized olives from each stand. Each probe consisted of an ellipsoid made of Teflon plumbing tape attached to one end of a wooden dowel. A total of 9 probes were created. The probes were measured to the tenth of a millimeter using digimatic calipers and created to incrementally span the range of average fruit sizes from the study stands. Because we used Teflon tape instead of a rigid or brittle substance, the probes had a smooth and slightly flexible surface, which to the touch resembled the surface of ripe *Olea* fruits and yielded similarly (slightly) when squeezed in the hand. We wrapped the Teflon tape as tightly as possible to create surface tension, mimicking the firmness of a full, ripe fruit.

We obtained previously-frozen, whole frugivorous bird carcasses from the University of California, Davis, Wildlife Museum. Once they had thawed, all carcasses were in good condition; we used none that had dried or otherwise stiffened, and all had mouths and esophagi that were open and unobstructed. The use of such carcasses instead of dried, prepared skins with closed mouths enabled us to both (a) reduce the risk of skin shrinkage that would alter measurements and mislead our conclusions, and (b) verify the ability of each bird to pass olives all the way through the esophagus and into the stomach. For each carcass, we measured the external bill gape width (bill width at the commissures) and the external maximum bill height (from the top to the bottom of the bill at its base). We then inserted each of the nine probes into each carcass's mouth to determine whether it could pass through the full esophagus to the stomach. We repeated this for up to 10 carcasses per bird species (depending upon availability). These trials generated a list of the stands containing fruits that could morphologically be dispersed by each tested bird species.

When all available carcasses (representing 18 species) had been tested, a few bird species remained that we believed to be candidates for olive dispersal (i.e., frugivorous in habit and occurring in olive stand sites) but that were not available as whole carcasses. These species included American crow (*Corvus brachyrhynchos*), California quail (*Callipepla californica*), northern mockingbird (*Mimus polyglottos*), spotted towhee (*Pipilo maculatus*), western meadowlark (*Sturnella neglecta*), and wild turkey (*Meleagris gallopavo*). Through logistic regression, we ascertained that external bill gape width was predictive of successful esophageal passage of all probes ($P < 0.0001$). We thus measured external gape width of prepared museum specimens of the remaining candidate bird species to determine which stands they are capable of dispersing. We used 10 museum specimens each for these species except when fewer than 10 were available (the museum owned only four turkey specimens, and all were used). All measurements were taken at the commissures and therefore relevant to the hard bill dimensions rather than skin dimensions; nevertheless, some drying and shrinkage could occur on study skins during their preparation. In light of our hypotheses (that a greater number of bird species should feasibly disperse fruits of smaller size), any shrinkage that may have led us to falsely conclude a negative (that a given bird species could not disperse a given fruit size) would lead us to underestimate the number of species capable of dispersal, making our approach conservative.

In winter, 2008–2009, we conducted bird counts at 70 points in each of the four study sites. Each count lasted seven minutes. At each point, all birds detected by sight or sound were recorded by species and number of individuals. To compare population densities among birds of smaller and larger body size, we examined point count results truncated at 25 m from the point (i.e., only birds detected within a 25-m radius of the point, or an area of 1963.5 m^2, were included in analyses). We calculated the density of detections (number of individuals per hectare) for each of the 22 potential disperser species identified by the esophageal probes and logistic regression. We then performed two linear regressions: first, we regressed the number of potential dispersers on the minimum fruit width to determine whether there was a significant increase in the size of potential disperser suites as minimum olive size decreased across stands. Second, we regressed the total density of detections of potential disperser species on the minimum fruit width to determine whether the density of total potential dispersers, across all species, increased more rapidly than did the diversity of dispersers as minimum olive size decreased. To compare slopes between the two regressions, we used proportional values, angular-transformed to meet regression assumptions, and graphed them together in the same space.

All statistical analyses were performed in JMP 5.0 (SAS Institute Inc., Cary, NC). Significance was accepted at $P \leq 0.05$.

TABLE 2. BIRD SPECIES CAPABLE OF SWALLOWING *OLEA EUROPAEA* FRUITS FROM EACH STUDY STAND, BASED ON AVERAGE GAPE WIDTH MEASUREMENTS, GAPE WIDTH PROBES, AND AVERAGE OLIVE WIDTHS. Ave. olive widths are means (mm) ±1 SE. Min. olive widths are minimum widths (mm) obtained in a random selection of 30 olives per stand. Gape width probes were used on frozen, whole carcasses to test esophageal passage of various fruit sizes for most bird species. For six bird species (AMCR, CAQU, NOMO, SPTO, WEME, WITU), no whole carcasses were available; stand list is based instead on external measurements and logistic regression results ($P < 0.0001$). [a]Bird abbreviations: AMCR = American crow; AMRO = American robin; CAQU = California quail; CEWA = cedar waxwing; EUST = European starling; GCSP = golden-crowned sparrow; HETH = hermit thrush; HOFI = house finch; HOSP = house sparrow; MODO = mourning dove; NOFL = northern flicker; NOMO = northern mockingbird; SPTO = spotted towhee; STJA = Stellar's jay; SWTH = Swainson's thrush; VATH = varied thrush; WCSP = white-crowned sparrow; WEBL = western bluebird; WEME = western meadowlark; WITU = wild turkey; WSJA = western-scrub jay; YBMA = yellow-billed magpie.

Study stand	Ave. width	Min. width	Potential dispersers[a] (average olive)	Potential dispersers[a] (minimum olive)
1	9.68 ± 0.21	5.61	AMCR, AMRO, CAQU, CEWA, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, GCSP, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WCSP, WEBL, WEME, WITU, WSJA, YBMA
2	9.93 ± 0.11	6.52	AMCR, AMRO, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
3	12.19 ± 0.56	7.60	AMCR, AMRO, EUST, NOFL, STJA, VATH, WEME, WITU, YBMA	AMCR, AMRO, CAQU, CEWA, EUST, HETH, HOFI, HOSP, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
4	15.15 ± 0.41	9.13	AMCR, EUST, YBMA, WITU	AMCR, AMRO, CAQU, CEWA, EUST, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
5	14.07 ± 0.49	9.14	AMCR, WITU	AMCR, AMRO, CAQU, CEWA, EUST, HETH, MODO, NOFL, NOMO, SPTO, STJA, SWTH, VATH, WEBL, WEME, WITU, WSJA, YBMA
6	14.50 ± 0.19	10.24	AMCR, EUST, WITU, YBMA	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
7	17.79 ± 0.23	11.12	AMCR, WITU	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
8	15.45 ± 0.17	11.39	AMCR, EUST, WITU, YBMA	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
9	16.10 ± 0.26	11.50	AMCR, WITU	AMCR, AMRO, EUST, NOFL, SPTO, STJA, VATH, WEME, WITU, YBMA
10	18.57 ± 0.36	12.29	AMCR, WITU	AMCR, AMRO, EUST, NOFL, STJA, VATH, WEME, WITU, YBMA
11	17.37 ± 0.26	12.72	AMCR, WITU	AMCR, EUST, WITU, YBMA
12	20.28 ± 0.51	13.02	AMCR, WITU	AMCR, EUST, WITU, YBMA

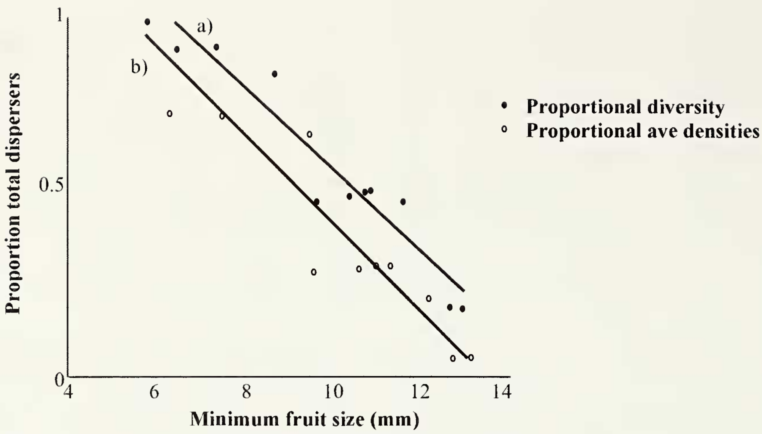

FIG. 1. Graph comparing the slopes of regressions between (a) proportion of total disperser species and minimum fruit width, and (b) proportion of average total disperser densities and minimum fruit width. Original data values are presented here, but arcsine-transformed values were used in statistical analysis. Average total number of disperser individuals accumulates at a slightly greater rate as fruit width decreases than does the total number of disperser species. However, the slopes between the two regressions are not significantly different.

Results

From esophageal probes and gape width measurements, we developed a list of birds that are anatomically capable of swallowing average- and minimum-sized *Olea* fruits from each study stand (Table 2). Only two species (American crow and wild turkey) are likely capable of dispersing average fruits from the largest-fruited stands, but additional species would be capable of consuming the smallest fruits from even these stands (Table 2).

There was no significant relationship between land use type and fruit size ($P = 0.19$). The smallest fruit sizes (both average and minimum) were found in the only feral population we were able to study. Across study stands, those with the smallest fruits and correspondingly greatest number of potential dispersers occurred in semi-natural or urban locations. The maximum number of potential dispersers for any stand was 17 bird species likely capable of swallowing average-sized fruits and 22 species capable of swallowing minimum-sized fruits (Table 2). Two bird species (golden-crowned sparrow, *Zonotrichia atricapilla*, and white-crowned sparrow, *Zonotrichia leucophrys*) were capable of swallowing only fruits of the smallest-fruited stand. When stands are ranked by their fruit sizes, a threshold can be observed between stands 3 and 4: twelve bird species capable of swallowing fruits from the three smallest-fruited stands have gape widths too small to accommodate fruits from the remaining nine stands (Table 2). Only 10 bird species appear capable of consuming fruits from those larger-fruited stands.

By linear regression, the relationship between number of potential disperser species and minimum olive size was highly significant ($R^2 = 0.90$; $P < 0.0001$) and negative, confirming that disperser suites become larger as olive sizes shrink. The regression between average density of potential disperser species and minimum olive size was also highly significant ($R^2 = 0.92$; $P < 0.0001$). The slope of the density regression was slightly steeper than that of the richness regression (ratio of slopes = 1.09) (Fig. 1). However, the slopes were not significantly different.

Discussion

In *Olea europaea*'s native range, birds shift from swallowing fruits to pecking them when gape width limits whole fruit ingestion (Rey and Gutiérrez 1996; Rey et al. 1997). We frequently observed western meadowlarks, European starlings (*Sturnus vulgaris*), and American robins (*Turdus migratorius*) selecting fruits on the ground beneath olive trees and attempting to swallow them by repeatedly grasping them in the beak and dropping them before resorting to pecking or moving on to swallow a smaller fruit. Logically, small-fruited feral populations resulting from bird selection may be facilitated by both this disproportionate selection of smaller fruits among larger ones and by increased visitation to small-fruited stands relative to large-fruited stands.

Our results demonstrated that smaller probes could pass through the esophagi of a wider diversity of bird species. This illustrates the anatomical mechanism enabling larger suites of potential dispersers for small-fruited populations. The only truly feral stand we examined (Stand 1) did indeed have the smallest fruits of all of our observed stands. This feral stand is located in Chico, Butte Co., CA, in a zone approximately 1 km^2 in area where *Olea* individuals are visibly spreading up-canyon from a century-old population cultivated at the edge of a municipal golf course. Individuals in this feral stand are clustered beneath perch sites such as larger trees and power lines. Birds thus appear to be mediators of this localized invasion.

Our results are not sufficient to conclude that bird-mediated dispersal in California directly results in small-fruited feral *Olea* populations because we were unable to replicate this work in multiple feral stands due to their rarity and land jurisdictions. Instead, our study demonstrates the higher potential for bird-mediated dispersal of small *Olea* fruits relative to large fruits. Land managers in California should be alert to the establishment of feral *Olea* trees with small fruits, since these have a higher probability of becoming sources of species spread than would large-fruited conspecifics. Whether such small fruits result from lack of care, irrigation, and cultivation or from bird-mediated selection, a wider variety of birds and a greater number of birds may be expected to visit such stands and to disperse fruits than occurs for large-fruited trees.

A dramatic decrease in the diversity of potential dispersers can be seen when comparing study stands 1 through 3 with the remaining stands. Evidently, the minimum fruit size increase between stands 3 and 4 represents the crossing of a size threshold. Fruits smaller than this threshold have more than twice the dispersal potential (in terms of the number of species able to carry out dispersal) of fruits larger than this threshold. If small *Olea* fruits become more common in California as a result of feralization, we expect that a greater rate of bird-mediated dispersal is likely to manifest in the region. As long as no other factors (e.g., unsuitable soils, herbivory, or competition) serve as barriers to establishment, such a marked boost to a spread mechanism could propel *Olea* out of a lag phase and into overt regional invasiveness.

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